AD-A270 214

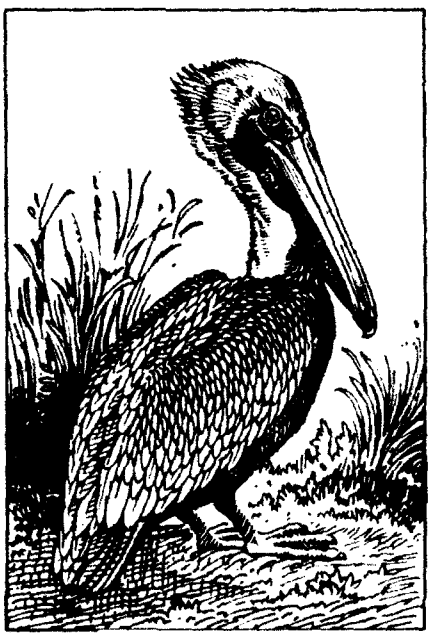
US Army Corps of Engineers
Waterways Experiment Station

Wetlands Research Program Technical Report WRP-DE-5

Factors Controlling the Formation of Oxidized Root Channels: A Review and Annotated Bibliography

by Irving A. Mendelssohn

DTIC
S ELECTE D
OCT 0 6 1993
A



93-23358
93 10 5 139

August 1993 – Final Report
Approved For Public Release; Distribution Is Unlimited

The following two letters used as part of the number designating technical reports of research published under the Wetlands Research Program identify the area under which the report was prepared

	Task		Task
CP	Critical Processes	RE	Restoration & Establishment
DE	Delineation & Evaluation	SM	Stewardship & Management

The contents of this report are not to be used for advertising, publication, or promotional purposes. Citation of trade names does not constitute an official endorsement or approval of the use of such commercial products.

PRINTED ON RECYCLED PAPER

Wetland Delineation Hydrologic Indicators

Factors Controlling the Formation of Oxidized Root Channels: A Review and Annotated Bibliography (TR WRP-DE-5)

ISSUE:

In spite of the importance of wetland hydrology in wetland delineation, quantitative data on the hydrology of a particular wetland is rarely available. One of the field indicators used in lieu of quantitative data is the presence of oxidized root channels (rhizospheres) associated with living roots and rhizomes. Little information exists about the environmental and biotic factors that cause oxidized root channels to form or how reliable they are as an indicator of wetland hydrology.

RESEARCH:

The primary objectives of this report were to provide an annotated bibliography of literature concerning root iron deposits that visually result in oxidized root channels, to describe and evaluate the current state of knowledge of the factors controlling the formation of iron plaques, and to recommend research to address the information gaps.

SUMMARY:

The most important abiotic and biotic factors controlling the presence and degree of iron plaque formation are the availability of soil iron and the oxidizing capacity of the plant root, respectively. Oxidized root channels indicate that soil saturation for a sufficient period to produce anaerobic conditions occurred within the life span of the plant root. However, until more is known about the relative abilities of different plant species to produce oxidized root channels, the temporal persistence of root iron plaques, and the role of soil chemistry, the absence of oxidized root channels, in itself, should not be used to indicate the absence of a wetland.

AVAILABILITY OF REPORT:

The report is available on Interlibrary Loan Service from the U.S. Army Engineer Waterways Experiment Station (WES) Library, telephone (601) 634-2355.

To purchase a copy, call the National Technical Information Service (NTIS) at (703) 487-4650. For help in identifying a title for sale, call (703) 487-4780. NTIS report numbers may also be requested from the WES librarians.

About the Author:

The author of this report is Dr. Irving A. Mendelssohn, who is a coastal plant ecologist and professor within the Wetland Biogeochemistry Institute and the Department of Oceanography and Coastal Sciences at Louisiana State University. Point of contact at WES is Barbara A. Kleiss, U.S. Army Engineer Waterways Experiment Station, ATTN: CEWES-ER-W, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199, Phone (601) 634-3836.

Please reproduce this page locally, as needed.

Wetlands Research Program

Technical Report WRP-DE-5
August 1993

Factors Controlling the Formation of Oxidized Root Channels: A Review and Annotated Bibliography

by Irving A. Mendelssohn
Wetland Biogeochemistry Institute

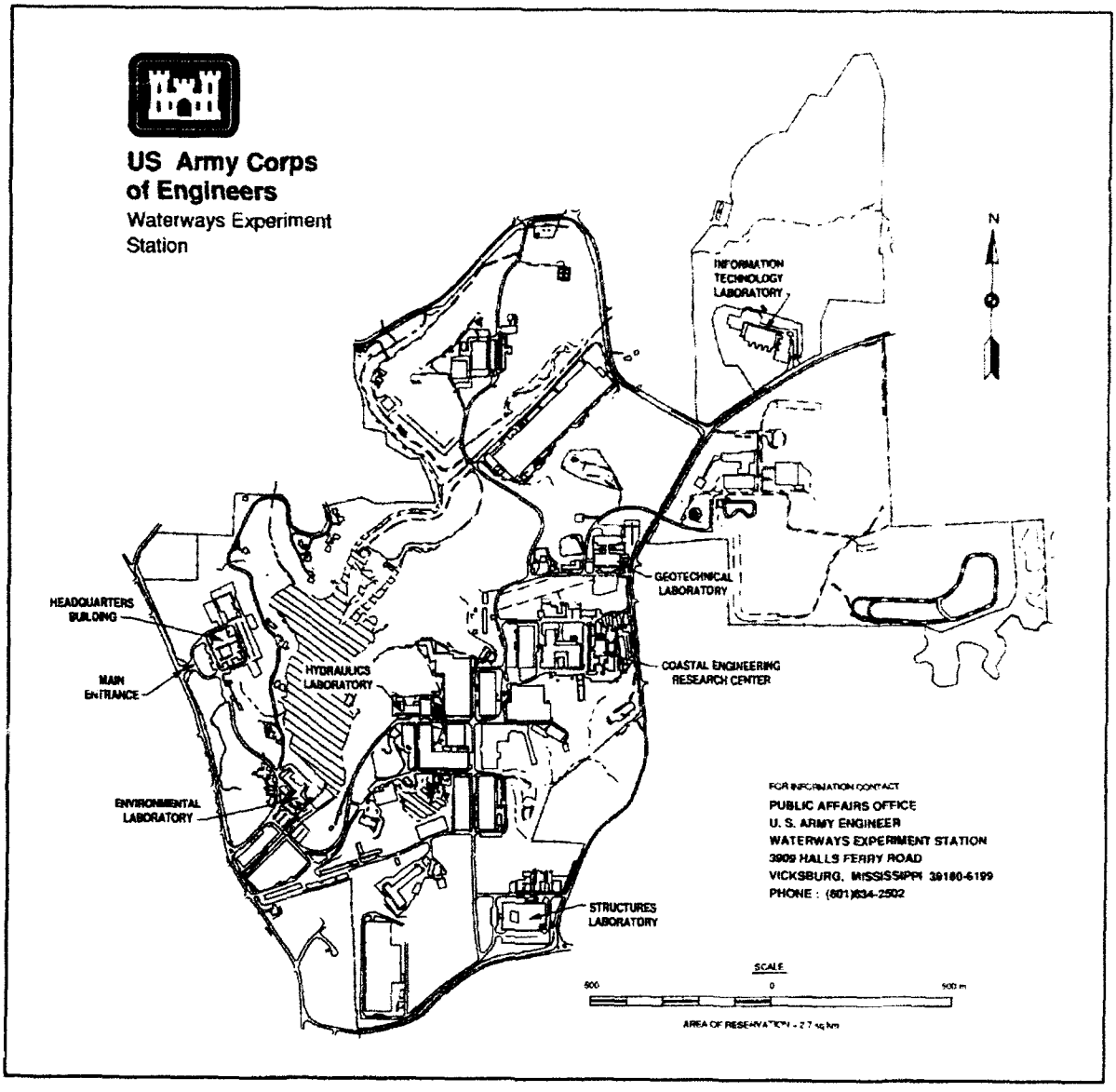
Center for Coastal, Energy and Environmental Resources
Louisiana State University
Baton Rouge, LA 70803

Accession For
NTIS CRA&I ☒
DTIC TAB ☐
Unannounced ☐
Justification
By
Distribution/
Availability Codes
Dist | Avail and/or Special
A-1

Final report

Approved for public release; distribution is unlimited

Prepared for U.S. Army Corps of Engineers
Washington, DC 20314-1000
Under WRP Work Unit 32755
Monitored by Environmental Laboratory
U.S. Army Engineer Waterways Experiment Station
3909 Halls Ferry Road, Vicksburg, MS 39180-6199



Waterways Experiment Station Cataloging-in-Publication Data

Mendelssohn, I. A.

Factors controlling the formation of oxidized root channels : a review and annotated bibliography / by Irving A. Mendelssohn ; prepared for U.S. Army Corps of Engineers ; monitored by Environmental Laboratory, U.S. Army Engineer Waterways Experiment Station.

36 p. : ill. ; 28 cm. -- (Technical report ; WRP-DE-5)

Includes bibliography.

1. Aquatic plants -- Roots -- Bibliography. 2. Roots (Botany) -- Bibliography 3. Wetland ecology. 4. Soils -- Iron content -- Environmental aspects. I. United States. Army. Corps of Engineers. II. U.S. Army Engineer Waterways Experiment Station. III. Wetlands Research Program (U.S.) IV. Title. V. Series: Wetlands Research Program technical report ; WRP-DE-5. VI Series: Technical report (U.S. Army Engineer Waterways Experiment Station) ; WRP-DE-5.

TA7 W34 no.WRP-DE-5

Contents

Preface vi

1—Introduction 1

2—Methods 3

3—Results 4

Factors Controlling Formation of Oxidized Root Channels 4
Mineralogy and formation of oxidized root channels 4
Mineralogy 4
Morphology 4
Plaque distribution 5
Time course of deposition 6
Biotic controls on oxidized root channel formation 6
Plant species and root radial oxygen loss 6
Root enzymatic oxidation 7
Rhizosphere bacteria 7
Soil physicochemical control of oxidized root channel formation 8
Iron concentration and source 8
Soil oxygen demand 9
Soil pH 10
Soil texture and organic matter 10
Soil fertility 11
Water conditions 11
Season 12
Summary of controls on plaque deposition 12
Recommendations for Future Research 14

4—Summary and Conclusions 15

References 17

Appendix A: Annotated Bibliography A1

SF 298

Preface

The work described in this report was authorized by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), as part of the Delineation and Evaluation Task Area of the Wetland Research Program (WRP). The work was performed under Work Unit 32755, "Wetland Delineation," for which Dr. James S. Wakeley was Principal Investigator. Mr. Sam Collinson (CECW-OR) was the WRP Technical Monitor for this work.

Mr. Jesse A. Pfeiffer, Jr. (CERD-C), was the WRP Coordinator at the Directorate of Research and Development, HQUSACE; Dr. William L. Klesch (CECW-PO) served as the WRP Technical Monitor's Representative; Dr. Russell F. Theriot, Environmental Laboratory (EL), U.S. Army Engineer Waterways Experiment Station (WES), was the Wetlands Program Manager. Mr. Ellis J. Clairain, Jr., Ecological Research Division (ERD), EL, was the Task Area Manager.

This report was prepared by Dr. Irving A. Mendelssohn, under contract No. DACW3990M3816. Dr. Mendelssohn is a professor at the Wetland Biogeochemistry Institute and the Department of Oceanography and Coastal Science at Louisiana State University. The work was performed under the direct supervision of Ms. Barbara A. Kleiss, Research Ecologist, Wetlands Branch, ERD, and under the general supervision of Mr. E. Carl Brown, Chief, Wetlands Branch, ERD, Dr. Conrad J. Kirby, Chief, ERD, Dr. John Keeley, Assistant Director, EL, and Dr. John Harrison, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

This report should be cited as follows:

> Mendelssohn, I. A. (1993). "Factors controlling the formation of oxidized root channels: A review and annotated bibliography," Technical Report WRP-DE-5, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

1 Introduction

Consistent with the Corps of Engineers and the U.S. Environmental Protection Agency's definition of wetlands, wetland delineation manuals have traditionally described a three-parameter approach for identifying wetlands. Wetlands have (a) hydric soils, (b) hydrophytic vegetation, and (c) wetland hydrology. All three parameters should be present before an area is considered to be a wetland. To meet the hydrology criterion, stream gage data, groundwater well data, or other direct observations of inundation or soil saturation are required. However, this criterion is problematic as quantitative hydrologic data are rarely available for sites where wetland determinations must be performed. In lieu of hydrologic data, field indicators are utilized that can be readily observed during a field inspection to satisfy the hydrology criterion when direct evidence is not available. The presence of oxidized root channels (rhizospheres) associated with living roots and rhizomes is one field indicator used to indicate the presence of wetland hydrology. Oxidized root channels appear as reddish brown or orangish areas that form halos around small roots and/or coatings on the root surface; these halos and coatings contrast clearly with the grayer color of the soil matrix.

Oxidized root channels result from the ability of hydrophytic vegetation to transport oxygen via air-space tissue (aerenchyma or lacunae) from the atmosphere through the plant to the roots and into the adjacent soil where iron oxyhydroxide (FeOOH) coatings or plaques can precipitate on and around the root. The assumption that these plaques are evidence of soil saturation or anaerobic conditions at the site for a significant period of time during the growing season has been the premise for their inclusion in various wetland delineation manuals as indicators of wetland hydrology. The basis for this assumption is that iron oxyhydroxide plaques occur when ferrous iron (Fe^{2+}), formed during periods of anaerobic soil conditions from the biochemical reduction of ferric iron (Fe^{3+}), is oxidized to iron oxyhydroxides because of radial oxygen release from plant roots. These plaques accumulate because soluble Fe^{2+} moves with groundwater or follows concentration gradients toward the sites of Fe^{3+} precipitation. Iron plaques would not be expected to form on and around roots under aerobic conditions because soil iron would already be in the ferric form and thus would not be affected by root oxygen loss. Thus, no root-induced iron precipitation would occur. In addition, oxygen release from the roots would be minimal because of lesser air space volume in plants

growing in aerated soils and lower rates of oxygen diffusion through the plant because of a more gradual oxygen gradient between the atmosphere and the soil.

In spite of the significant role this indicator can play in wetland identification, little information exists about the environmental and biotic factors that cause oxidized root channels to form or how reliable they are as an indicator of wetland hydrology. The objectives of this report are to (a) provide an annotated bibliography of literature concerning root iron deposits, (b) describe and evaluate the current state of knowledge of the factors controlling the formation of iron plaques, and (c) recommend research to address information gaps. The annotated bibliography presented in this report was not designed to be exhaustive, but rather to emphasize information specifically dealing with the formation of iron plaques on and around living roots and rhizomes, reported in refereed scientific journals. Nonrefereed reports were not included in the bibliography.

2 Methods

References on root iron plaques (also referred to as oxidized root channels, coatings, or deposits) were derived from the author's personal library augmented by computerized searches of the literature. In addition, the Literature Cited sections of all references retrieved from these sources were scrutinized for relevant references not identified in the computer searches.

Computer searches were conducted through the Louisiana State University Library. The following bibliographic databases were searched for pertinent citations:

a. Biosis Previews: This index contains citations from both Biological Abstracts and Biological Abstracts/RRM (formerly entitled Bioresearch Index), the major publications of Biosis. Over 9,000 primary journals and monographs, as well as symposia, reviews, selected institutional and government reports, and other secondary sources, are scanned for relevant citations. Coverage: 1969 to the present; file size: 6,665,720 citations.

b. CAB Abstracts: The Commonwealth Agricultural Bureaux Abstracts is a comprehensive file of agricultural and biological information containing all the records in the 26 main abstract journals published by Commonwealth Agricultural Bureaux. Over 8,500 journals in 37 different languages are scanned for inclusion, as well as books, reports, theses, conference proceedings, patents, annual reports, and guides. Coverage: 1972 to the present; file size: 2,435,880 citations.

c. AGRICOLA: AGRICOLA (formerly CAIN) is the database of the National Agricultural Library (NAL). This massive file provides comprehensive coverage of worldwide journal literature and monographs on agriculture and related subjects, including animal studies, botany, chemistry, entomology, fertilizers, forestry, hydrology, soils, and more. Coverage: 1970 to the present; file size: 2,654,155 citations.

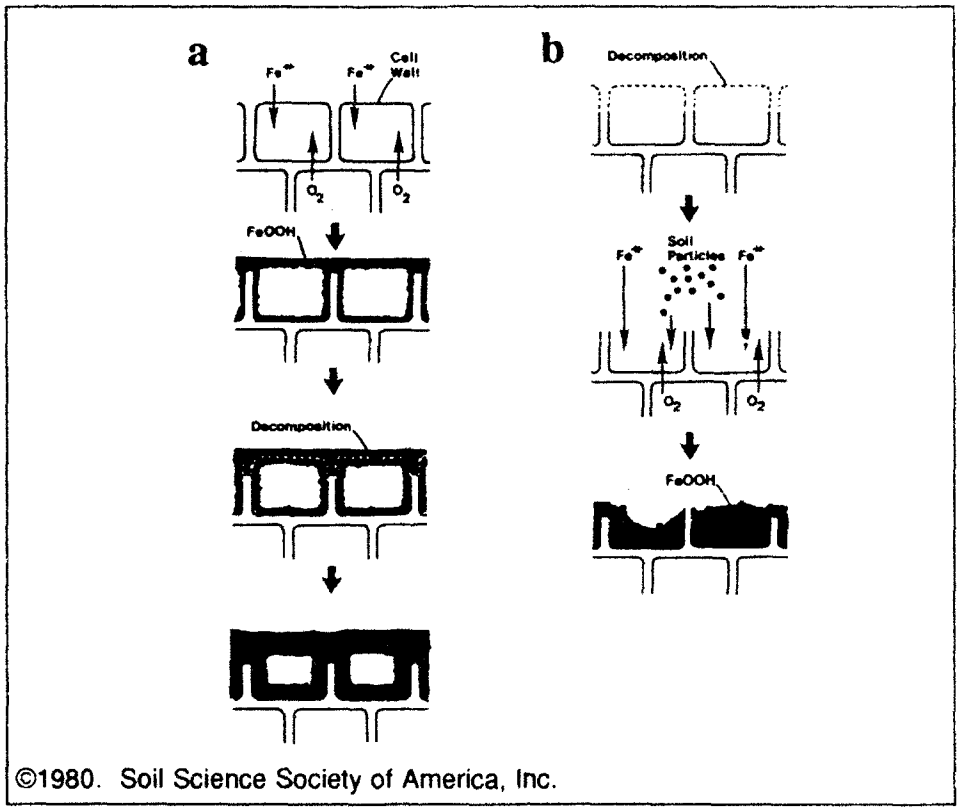
3 Results

Factors Controlling Formation of Oxidized Root Channels

Mineralogy and formation of oxidized root channels

Mineralogy. The oxidized deposits or plaques found on and around the roots of certain plants growing in saturated soils consist of two iron oxyhydroxide minerals: (a) lepidocrocite (gamma-FeOOH) and (b) goethite (alpha-FeOOH) (Bacha and Hossner 1977; Chen, Dixon, and Turner 1980a). Bacha and Hossner (1977) found only lepidocrocite on rice roots grown in the laboratory in sand containing iron chloride at a pH of 6 to 7. In contrast, Chen, Dixon, and Turner (1980b) identified both lepidocrocite and goethite on field-grown rice roots. This was the first time that goethite had been observed as root deposits. The authors hypothesized that the presence of goethite may be due to the following: (a) rapid oxidation of Fe^{2+} causes lepidocrocite to form initially, but in time it dissolves and the more stable goethite forms, (b) high carbon dioxide (CO_2) in soil favors goethite over lepidocrocite, and (c) aluminum in solution suppresses the formation of lepidocrocite and goethite tends to form. Some or all of these factors may control the ratio of goethite to lepidocrocite in oxidized root channels.

Morphology. Root iron plaques occur primarily as fillings or casts in exposed cavities of epidermal cells (Chen, Dixon, and Turner 1980a). Two models for cast formation, based on whether iron precipitation occurs before or after cell wall decomposition, were presented by Chen, Dixon, and Turner (1980a). This difference in mode of formation explains the observed differences in cast morphology: (a) hollow interior, smooth surface, and polyhedral casts and (b) solid porous interior, rough surface, and polyhedral casts. In both cases, the epidermal cell walls provide a template for development of the cast as iron precipitates on and in the outer epidermal cell. The hollow interior cast forms when iron precipitation occurs before the decomposition of the outer cell wall, while the solid interior cast forms after the outer cell wall has degraded (Figure 1). The rough surface of the solid interior cast presumably results from soil particles adhering to the cast outer surface and because the cast was not formed against a smooth template, i.e., the outer cell wall of the



©1980. Soil Science Society of America, Inc.

Figure 1. Two hypothetical models for iron plaque development. (a) Plaque forms before cell wall decomposition. (b) Plaque forms after cell wall decomposition (from Chen, Dixon, and Turner (1980a)) (used by permission)

epidermis (Chen, Dixon, and Turner 1980a). Oxidized root channels that form adjacent to roots result from the precipitation of iron on soil particulates.

Plaque distribution. The interior root penetration of iron deposition is variable. Mendelssohn and Postek (1982), using scanning electron microscopy and X-ray microanalysis, determined that the iron coated only the outer cell wall of the root epidermis of the salt marsh grass *Spartina alterniflora*. Although Tanaka, Loe, and Navasero (1966) found similar patterns in rice (*Oryza sativa*), Green and Etherington (1977) identified precipitated iron as far into the rice root as the cell walls and intercellular spaces of the outer cortex. Taylor, Crowder, and Rodden (1984) obtained similar results in *Typha latifolia*. Differences in plaque penetration of the root may result from variance in the extent of the oxidized rhizosphere because of differential root radial oxygen loss among species (or between experiments with the same species), differences in root respiration, and/or different soil oxygen demands of the rooting medium (Takijima 1965; Armstrong 1971; St-Cyr and Crowder 1989).

The distribution of iron plaque formation on the root appears to match the regions of the root where intense radial oxygen loss occurs. Taylor, Crowder, and Rodden (1984) found that the most heavily stained portions of *Typha* roots were approximately 1 cm above the root tip, extending for variable lengths up the root, and matching the regions of intense oxygen efflux as described by Armstrong (1971).

Time course of deposition. Iron deposition on rice roots occurs quickly. Rice root coatings were present after only 7 days of field flooding (Chen, Dixon, and Turner 1980a) and after 11 days in an agar substrate containing iron sulfide (Trolldenier 1988). To the author's knowledge, a true time-course examination of the rate of iron plaque formation has not been conducted.

Biotic controls on oxidized root channel formation

Plant species and root radial oxygen loss. A primary factor controlling the formation of oxidized root deposits is the ability of the particular plant species to transport oxygen from the atmosphere through the plant into the roots and out into the surrounding soil. Many flood-tolerant plants are capable of oxygen transport as a result of air-space tissue (aerenchyma or lacunae), consisting of dead cells or cavities between cells, which create a conduit for oxygen movement along a concentration gradient through the plant into the anaerobic flooded soil. Thus, only those plant species that demonstrate oxygen transport and root radial oxygen loss can potentially form oxidized root channels in the soil. However, some plants exhibit root enzymatic oxidation which may also cause the formation of an oxidized rhizosphere around the root (Armstrong 1967a).

Although root radial oxygen loss appears essential for root plaque formation to occur (Chen, Dixon, and Turner 1980b), the relationship between the degree of radial oxygen loss and the amount of iron plaque formation is not always good. For example, Wright and Hossner (1984) investigated the radial oxygen loss in six varieties of rice and found no statistically significant correlation between oxygen release rates and root iron coatings, although the variety "Belle Patna" had the highest radial oxygen release and the greatest iron deposition of the six varieties. These findings are supported by Laan et al. (1989) for three species of *Rumex*. *Rumex thyrsiflorus*, the species with the lowest root radial oxygen loss, had the most plaque. Thus, although radial oxygen loss is certainly important in allowing plaque formation and in some instances is directly related to plaque accumulation (Chen, Dixon, and Turner 1980b), additional factors (see below) can modify and, in certain cases, obscure this relationship.

Only a relatively small number of plant species have been shown to generate oxidized root channels. These species include the following: *Oryza sativa* (Tanaka, Loe, and Navasero 1966; Armstrong 1967a; Howeler 1973; Green and Etherington 1977; Chen, Dixon, and Turner 1980a, 1980b; Boone, Bristow, and van Loon 1983; Wright and Hossner 1984; Trolldenier 1988),

Typha latifolia (Taylor, Crowder, and Rodden 1984; Crowder and Macfie 1986), *Phragmites australis* (Taylor and Crowder 1983; St-Cyr and Crowder 1987, 1988, 1989, 1990), *Aster tripolium* (Otte et al. 1989), *Spartina alterniflora* (Mendelssohn and Postek 1982), *Spartina maritima* (Vale et al. 1988), and *Molinia caerulea, Menyanthes trifoliata, Narthecium sp., Carex rostrata, Phragmites communis, Myrica gale,* and *Potomogeton polygonifolius* (Armstrong and Boatman 1967). These studies specifically observed and/or identified iron plaque deposits on the roots of these plants. However, as noted above, species-specific differences in iron plaque accumulation occur. Crowder and Macfie (1986) demonstrated that of three species growing in the same wetland in Canada, *Carex rostrata* accumulated plaque at a greater rate and to a higher level than did *Typha latifolia*; *Phragmites australis* was intermediate. In Bartlett's (1961) study of the root oxidizing capacity of several different forage crops and natural herbs, reed canary grass, timothy, and trefoil were consistently among the most successful oxidizers; red clover and bromegrass had lesser ability; and alfalfa had the lowest oxidizing ability (scientific names were not given in the original manuscript).

A large number of studies have independently demonstrated radial oxygen loss in various plant species (van Raalte 1944; Coult and Vallance 1958; Armstrong 1964, 1967b, and 1968; Takajima 1965; Joshi, Ibrahim, and Hollis 1973; Armstrong and Armstrong 1988; Laan et al. 1989; and numerous others). However, these studies are beyond the scope of this review, which concentrates specifically on iron plaque formation.

Root enzymatic oxidation. Although most research implicates oxygen evolution as the primary cause for iron oxidation in the rhizosphere, Armstrong (1967a) determined that radial oxygen loss could account for only one-ninth of the total oxidizing capacity of rice roots. Thus, other sources of oxygen may contribute to rhizosphere oxidation of iron. Oxygen derived from root metabolism, for example, has been suggested as a contributor to this process (Mitsui et al. 1962; Takijima 1965). Mitsui et al. (1962) identified the enzyme glycolic acid oxidase in the roots of rice and suggested that this oxidase may be a source of rhizosphere oxygen; however, no direct test of this hypothesis was conducted.

Rhizosphere bacteria. Rhizosphere bacteria may represent a third cause of iron oxidation in the root rhizosphere. For example, Trolldenier (1988) observed extensive spherical colony-like structures, resembling bacteria, in association with iron deposits in the rhizosphere and on the root surface of rice. When these spherical structures were transferred to dilution tubes containing semisolid iron sulfide agar, reddish brown colonies developed, supporting the bacterial nature of these spherical structures. In the absence of the inoculant, the reddish brown colonies appeared in lesser abundance. Whether these colonies are actually iron-oxidizing bacteria is not known, although iron-oxidizing or precipitating bacteria have been found in the surface films of swamps (Ghiorse 1984). However, Trolldenier (1988) also found iron plaque formation in the root hair zone where no bacterial interaction was observed. Thus, it appears that bacteria are not a prerequisite for ferric iron precipitation.

In contrast to these findings, Johnson-Green (1988) found no evidence that rhizosphere bacteria contribute to iron oxidation. This is a fertile area for future research.

Soil physicochemical control of oxidized root channel formation

The most important soil-related factors that control iron plaque formation are (a) iron concentration and form, (b) soil oxygen demand, (c) soil texture and organic matter content, and (d) soil pH.

Iron concentration and source. A number of studies have documented that iron deposition on root surfaces results as iron concentration in solution increases and that the degree of deposition is directly related to iron concentration (Howeler 1973; Bacha and Hossner 1977; Taylor, Crowder, and Rodden 1984). For example, as concentration of Fe^{2+} increased from 0 to 100 ppm in solution, root iron deposits (extracted from the roots of *Typha latifolia* with the dithionite-citrate-bicarbonate (DCB) technique) increased in a curvilinear fashion (Taylor, Crowder, and Rodden 1984). Significant plaque formation occurred at as little as 5 to 10 ppm Fe^{2+} in solution. However, an upper limit to iron plaque accumulation exists, probably determined by the surface area of the root.

The greatest degree of iron plaque accumulation occurs when the iron in solution is in the ferrous form (Boone, Bristow, and van Loon 1983; Taylor, Crowder, and Rodden 1984). Chelated iron, whether the iron is stabilized in its oxidized state such as in Fe-EDTA (ferric-ethylenediaminetetraacetic acid) and Fe-EDDHA (ferric-ethylenediamine di(o-hydroxy-phenyl acetic acid)) or in its reduced state such as in Fe-BPDS (ferrous-4,7-di[4-phenylsulfonate] 1,10-phenanthroline or bathophenanthroline disulfonic acid), results in little iron plaque formation compared with that occurring in the presence of ferrous (Fe^{2+}) iron in solution (Wallace et al. 1957; Boone, Bristow, and van Loon 1983; Taylor, Crowder, and Rodden 1984). These findings support the contention that plaque formation is dependent on the oxidation of Fe^{2+} to Fe^{3+}, because supplying iron as Fe^{3+}, Fe^{3+} chelates, or Fe^{2+} chelates produced less extensive plaques (Taylor, Crowder, and Rodden 1984). However, at a culture solution pH of 4.0 or below, iron in the ferric form can result in greater plaque formation than when in the ferrous form (Boone, Bristow, and van Loon 1983). At these low pH's, significant concentrations of ferric iron will be maintained in a soluble and/or homogeneously dispersed colloidal form. Boone, Bristow, and van Loon (1983) suggests that at these lower pH values, the reduction of ferric iron that occurs at the root surface generates most of the iron utilized by the plant. In rice, this root reductive activity at low pH may be due to the release of phenolic compounds resulting from the degradation of suberin- and lignin-containing cell walls of the exodermis and endodermis (Boone, Bristow, and van Loon 1983).

Recently, the fraction of the soil iron that is bound to carbonates has been shown to be related to the degree of iron plaque formation more closely than

other iron fractions, such as exchangeable iron, iron bound to mineral oxides, iron bound to organic substrate, and residual iron (St-Cyr and Crowder 1988). *Phragmites australis* plants and associated soil and roots were collected from six sampling sites ranging from dry land to wetland in southern Ontario and Quebec, Canada. Soil iron in these samples was subdivided into the five main fractions via a sequential extraction procedure (St-Cyr and Crowder 1988) and these fractions examined for relationships with the amount of root iron plaque. The only statistically significant correlation was with the iron-bound-to-carbonate fraction of the soil iron. Interestingly, the exchangeable iron fraction, mainly represented by Fe^{2+} in the wetland habitats, was not significantly correlated with iron plaque formation. This result was unexpected as a number of laboratory studies (Bacha and Hossner 1977; Taylor, Crowder, and Rodden 1984) have shown that plaque formation is directly related to Fe^{2+} in solution. St-Cyr and Crowder (1988) reasoned that Fe^{2+} is not directly oxidized to iron oxyhydroxide plaques, but rather exchangeable iron must first be transformed to iron carbonates, specifically siderite ($FeCO_3$), a mineral identified in freshwater swamp sediments. Siderite is then oxidized in the rhizosphere to lepidocrocite and/or goethite depending on the rate of oxidation and hydrolysis (rapid oxidation favors lepidocrocite) and the concentration of CO_2 (high CO_2 favors goethite) (Schwertmann and Thalmann 1976; Schwertmann and Taylor 1977). The results of this oxidation are iron plaque formation. This mechanism could explain why exchangeable iron was not directly correlated with iron plaque accumulation. However, the possibility exists that some other factor, rather than available iron, limited plaque formation in this freshwater wetland. Also, one may question whether the exchangeable iron soil fraction as operationally defined in St-Cyr and Crowder (1988) adequately represents available iron. Research designed specifically to demonstrate the cause and effect relationship between iron-bound-to-carbonates and iron plaque formation and studies in other wetland systems are necessary before this mechanism of iron plaque formation can be unequivocally accepted.

Soil oxygen demand. Because iron solubility increases with decreasing soil redox potential (Eh), one might hypothesize greater plaque formation under more reduced conditions. Although no investigations have directly varied Eh and determined the extent to which root iron plaque formation changes, correlative data indicate the opposite trend. The higher (more positive) the soil Eh, up to a point, the greater the plaque formation (Taylor, Crowder, and Rodden 1984). However, if the Eh increases to a degree that greatly decreases the concentration of iron in solution (Gambrell and Patrick 1978), plaque formation will likely decrease depending on the soil pH (see pH discussion below). At the opposite end of the Eh range, a highly negative Eh will generate such an intense soil oxygen demand that the oxidizing capacity of the root will likely be overwhelmed, resulting in the absence of plaques. The fact that both very high and very low soil Eh's will likely prevent plaque formation explains why a field investigation of iron plaque formation in wetland plants did not demonstrate a relationship between site Eh and plaque accumulation (Crowder and Macfie 1986).

Soil pH. The pH of the soil can affect iron plaque formation directly by controlling the concentration of iron in solution and the resolubilization of precipitated root iron, and indirectly by influencing the net oxidizing capacity of the root.

Iron plaque formation on the roots of *Typha latifolia* linearly increased with solution pH from 3.0 to 4.6 (Taylor, Crowder, and Rodden 1984), probably because of the decreased solubility of the precipitated Fe^{3+} on the roots. These results support similar findings for rice, i.e., an increase in plaque accumulation between pH 3.0 and 5.3 (Boone, Bristow, and van Loon 1983). However for *Typha*, less plaque accumulation occurred above pH 5.0 than at pH 4.6, presumably because oxidation of Fe^{2+} in the culture solution reduced soluble iron and hence precipitation of iron on the root surfaces (Taylor, Crowder, and Rodden 1984). St-Cyr and Crowder (1989) also demonstrated that above pH 5, iron plaque accumulation on the roots of field-collected *Phragmites australis* decreased. However, in this case, the lower plaque accumulation at higher pH's was positively correlated with less iron in the iron-bound-to-carbonate fraction that, as mentioned above, may be the precursor to iron oxyhydroxide formation on the roots of this species (St-Cyr and Crowder 1988). An alternate explanation for this finding, however, is that at higher pH's, less soluble iron is in solution and, hence, there is less iron to form plaques.

Boone, Bristow, and van Loon (1983) presented data supporting the concept that pH can control the net oxidizing capacity of the rice root, and hence the ability to precipitate iron in the rhizosphere. The net oxidative or reductive nature of the rhizosphere will depend on the relative quantities and reactivities of the reductants and oxidants influencing the rhizosphere (Boone, Bristow, and van Loon 1983). With decreasing pH, the hydrolysis of suberin and lignin in the cell walls of the endodermis and exodermis of rice can result in the release of phenolic compounds that act as Fe^{3+} reducing agents. In addition, the rate of oxidation of Fe^{2+} decreases with decreasing pH. Thus at low pH, the rice root has a high reductive capacity that will tend to counterbalance its oxidative capacity, resulting in negligible iron plaque accumulation. As the soil pH increases, the net ability to oxidize the rhizosphere can increase, and plaque formation can proceed until the pH is too high to allow for iron to exist in solution, preventing plaque formation (Boone, Bristow, and van Loon 1983).

Soil texture and organic matter. Soil texture (percentages of sand, silt, and clay) and organic matter content are important factors in determining the extent of iron plaque formation. Chen, Dixon, and Turner (1980b) found that in soils with high clay content (Lake Charles and Beaumont soils) iron plaque deposition on rice roots was less than for soils with low clay content (Crowley and Katy). They hypothesized that the high clay soils bound more iron, making it less available, and developed lower Eh conditions, counterbalancing the oxidative power of the roots than soils with lower clay content. However, fine-textured mineral soils are an important source of iron. For example, more iron oxyhydroxide precipitates accumulated on rice roots growing in a Crowley

fine sandy loam than in pure sand where substrate iron limited plaque formation (Bacha and Hossner 1977).

Soil organic matter can modify the effect of clay content on iron plaque formation (St-Cyr and Crowder 1989). As mentioned previously, the iron-bound-to-carbonate fraction of the soil iron is related to the degree of plaque formation on the roots of *Phragmites australis* in various habitats in southern Canada (St-Cyr and Crowder 1988). In a subsequent investigation, St-Cyr and Crowder (1989) related various soil factors to the presence of iron-bound-to-carbonates. When partial correlation coefficients were employed, iron-bound-to-carbonates was positively correlated ($r = 0.865$, $P < 0.1$) with the percentage of clay when percentage of organic matter was constant and negatively correlated ($r = -0.823$, $P < 0.1$) with percentage of organic matter when clay content was constant. These results indicate a competition between clay and organic matter for iron. The authors proposed that clay can act as an iron reservoir, as suggested in Bacha and Hossner (1977), but iron liberated from the clay can be adsorbed to organic matter before being bound to carbonates in the soil. Thus, iron availability may be low in clay soils with high organic matter content, and as a result, plaque formation is limited (St-Cyr and Crowder 1989). Differences in soil organic matter may explain why Chen, Dixon, and Turner (1980b) found less plaque formation on rice roots growing in soils with higher clay content. Unfortunately, organic matter content of these soils was not reported.

Soil fertility. Although the effect of soil fertility on iron plaque formation has not been directly investigated, some general predictions are possible. Eutrophic conditions could intensify soil reduction (Eh) upon flooding, via accelerating microbial metabolism, and decrease the potential for iron oxyhydroxide precipitation on root surfaces. Conversely, higher concentrations of nutrients like nitrate or ferric iron could aid in poising the soil Eh and, thus, moderate the soil oxygen demand. However, if nutrient deficient conditions occurred, the oxidizing capacity of the roots might be reduced. For example, a silicon deficiency has been shown to reduce the oxidizing capacity of rice roots (Okuda and Takahashi 1965). A significant decrease in the surface area of oxidizing roots will also likely reduce plaque formation.

Water conditions. St-Cyr and Crowder (1989) found that of six field sampling sites, those adjacent to free-flowing water exhibited the greatest plaque formation on the roots of *Phragmites australis*. Since root plaque formation was closely associated with the iron-bound-to-carbonate fraction of the soil in these systems (St-Cyr and Crowder 1988), the authors suggested that the flowing water may be a source of carbonates, which could be derived from the drainage basin. These results explain the findings of Crowder and Macfie (1986), who demonstrated a seasonal increase in iron plaque accumulation on the roots of several wetland plants in only three of the seven habitats investigated. The three sites associated with a significant increase of the iron plaque were near a free-flowing water source. These results led St-Cyr and Crowder (1989) to suggest that iron plaque deposition on roots may be

site- and year-specific depending on variations in water movement and carbonate content.

Season. Iron plaque deposition may exhibit seasonal variation. Crowder and Macfie (1986) found that plaque accumulation on the roots of *Typha latifolia* increased rapidly in June and July, corresponding to peak biomass production of the shoots, and leveled off by late July and August. The authors attempted to explain the seasonal peak in plaque accumulation by suggesting that the concurrent seasonal peak in emergent biomass and photosynthesis provided oxygen for root radial oxygen loss and iron oxidation. However, it was interesting that this seasonal increase in iron plaque deposition occurred in only three of the seven wetlands sampled. Thus, plant biomass production could not have been the only factor controlling plaque formation. Site differences in soil Eh and pH as well as ecotypic differences in *Typha's* ability to produce iron coating were evaluated and ruled out as controlling site differences in plaque deposition (Crowder and Macfie 1986). However, as noted above, subsequent research (St-Cyr and Crowder 1989) points to the closeness of the wetland to free-flowing water and the carbonate contained within as the primary cause of this wetland-specific root iron deposition.

Iron oxyhydroxide deposition on field-grown rice roots has also been related to season and age of maturity (Chen, Dixon, and Turner 1980b). Accumulation of FeOOH was <2 percent of dry root weight after 7 days of soil flooding. It increased to a maximum of about 10 percent at plant maturity (ca. 110 days after emergence), and decreased slightly thereafter (Chen, Dixon, and Turner 1980b).

Photosynthesis has been suggested as a source of oxygen for iron deposition (Bartlett 1961; Crowder and Macfie 1986). This could explain some of the observed seasonal variation in plaque formation.

Summary of controls on plaque deposition

From the preceding discussion, one can determine that the controls on the formation of iron oxyhydroxide plaques can be very complex. Figure 2 summarizes these controls. The presence of soluble soil iron and plant species capable of creating an oxidized rhizosphere are probably the most important factors controlling plaque formation. The degree of available soil iron is inversely related to soil pH, Eh, and organic matter, but positively related to clay content. Plaque formation likely proceeds through either the oxidation of Fe^{2+} or siderite, the latter appearing important in some freshwater marshes. The greater the concentration of available iron, the greater the potential for siderite formation. Where soil calcium concentrations are high, calcite ($CaCO_3$), rather than siderite, can be the prevalent carbonate mineral, thus, reducing plaque formation via siderite. Plant roots likely oxidize either soluble Fe^{2+} or siderite to form plaques. Lepidocrocite and goethite are two iron oxyhydroxides that have been identified as comprising root plaques. The formation of lepidocrocite is favored during rapid oxidation and low CO_2

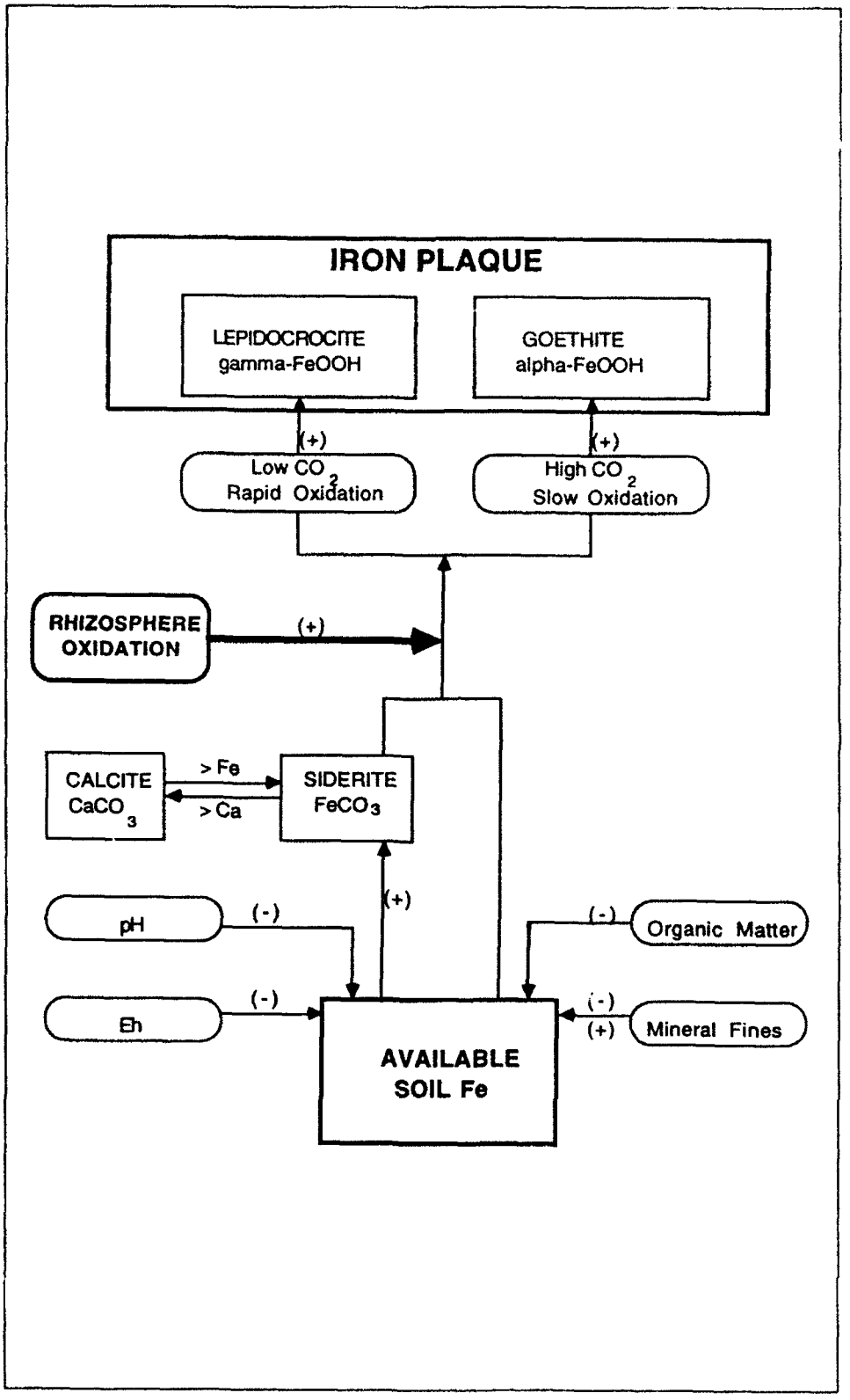


Figure 2. Conceptual model of factors controlling root iron plaque formation in an anaerobic soil. Pluses indicate positive relationships, while minuses denote negative relationships

conditions, while goethite formation is favored during slow oxidation and in a high CO_2 soil environment.

Recommendations for Future Research

Future research on iron plaque formation should concentrate on answering the following questions:

a. How universal is the phenomenon of hydrophyte-induced root plaque formation? Because only a handful of wetland plants have been identified as causing iron deposition, the species-specific nature of this process must be studied further.

b. What are the mechanisms by which oxidized root channels form? Are root iron oxide deposits formed primarily as a result of radial oxygen loss, enzymatic oxidation, and/or rhizosphere iron-oxidizing bacteria? Understanding the mechanism by which iron plaque formation occurs will aid in interpreting the significance of this hydrologic indicator.

c. What chemical fraction of the soil iron determines the degree of plaque accumulation? How does soil pH and Eh modulate this response? Although the iron-bound-to-carbonates fraction of the soil iron is closely related to iron plaque accumulation on the roots of *Phragmites australis* in southern Canada, the importance of this soil iron fraction in controlling root plaque formation has not been determined for other species and other wetland types. In addition, because pH and Eh generally control the solubility of iron in soils, the modulating effect of these factors should be determined.

d. How do other soil factors (texture, organic matter, and fertility) modify root plaque formation? These soil physicochemical parameters can change iron availability and root oxidizing potential and, in turn, the degree of iron plaque accumulation. A comprehensive understanding of the influence of these factors on iron plaque formation is essential before one can interpret the significance of root iron plaque formation under field conditions.

e. How do plant maturity and season control root iron plaque deposition? Iron plaques form as a result of the plant's ability to oxidize its rhizosphere in the presence of available iron in the flooded soil. Both of these factors, root oxidizing power and available iron, may seasonally vary.

4 Summary and Conclusions

The oxidized deposits or plaques observed on and around the roots of certain hydrophytic plants growing in saturated soils consist of two iron oxyhydroxide minerals: lepidocrocite (gamma-FeOOH) and goethite (alpha-FeOOH). These minerals are deposited both on the surface of the root and, in some cases, into the cell walls and intercellular spaces of the outer cortex. The distribution of the precipitated iron on the root surface often coincides with the zones of greatest root radial oxygen loss.

Both biotic and abiotic factors control the presence and degree of iron plaque formation. Biotic factors include the oxidizing power of the plant root via either radial oxygen loss and/or enzymatically derived oxygen, as well as the oxidizing potential of rhizosphere bacteria. Although most research in this field has concentrated on the importance of root radial oxygen loss in precipitating iron, only a very limited number of hydrophytic species have been evaluated for this trait. Thus, the relative ability of different species to produce root plaques must be identified. Furthermore, the importance of root enzymatic oxidation and bacterially induced oxidation in the process of iron plaque formation should be elucidated for a comprehensive understanding of the mechanisms controlling this process.

The most important abiotic factor determining the presence of oxidized root channels and iron plaque deposits is the availability of soil iron. Laboratory investigations have demonstrated that the concentration of ferrous iron (Fe^{2+}) in solution is directly related to the degree of root iron plaque accumulation. However, under field conditions, the iron-bound-to-carbonate fraction of the soil iron is better correlated with the amount of plaque formation than any other soil iron fraction including exchangeable ferrous iron. This relationship, however, has only been documented for *Phragmites australis* in freshwater wetlands of southern Canada. The particular soil iron fraction that determines root iron oxyhydroxide precipitation must be identified for a variety of wetland types and plant species.

Although the primary factors controlling iron plaque formation are the plant's ability to oxidize its rhizosphere and the presence of available iron in the soil, a number of soil physicochemical characteristics, including soil texture, organic matter, pH, Eh, soil fertility, and others, can secondarily determine the net oxidizing capacity of the root and/or the availability of iron for

oxidation and deposition on and around root surfaces. The competitive relationship between clay and organic matter and its interaction with soil pH and Eh in controlling the availability of soluble iron should be elucidated in a number of wetland types so that oxidized root channels can be used without ambiguity as an indicator of wetland hydrology. The effect of plant species in controlling plaque formation must also be addressed. In addition, the temporal persistence of the root iron plaque and the factors that control this persistence must be determined, as well as the significance of these coatings as indicators of the duration, frequency, and timing of soil saturation.

Unlike some of the other hydrologic indicators used in wetland delineation (e.g., water marks on trees or sediment deposits), root plaques and oxidized root channels indicate soil saturation for a sufficient period to produce anaerobic soil conditions. Additionally, when found in conjunction with a living root, oxidized root channels indicate that the anaerobic conditions occurred within the life span of the plant root, which is most likely within that growing season. Therefore, the presence of oxidized root channels and iron plaque surrounding living roots is a relatively good indicator of wetland hydrologic conditions. This conclusion is supported by one study in which the ratio of iron to manganese for root coatings proved to be a good predictor of soil wetness (Good, Faulkner, and Patrick 1986). However, until more is known about the relative abilities of different plant species to produce oxidized root channels, the temporal persistence of the root iron plaque, and the role soil chemistry plays in controlling plaque formation, the absence of oxidized root channels, in itself, should not be used to indicate the absence of a wetland.

References

Armstrong, J., and Armstrong, W. (1988). "*Phragmites australis*-a preliminary study of soil-oxidizing sites and internal gas transport pathways," *New Phytologist* 108, 373-382.

Armstrong, W. (1964). "Oxygen diffusion from the roots of some British bog plants," *Nature* 204, 801-802.

_____. (1967a). "The oxidizing activity of roots in water-logged soils," *Physiologia Plantarum* 20, 920-926.

_____. (1967b). "The use of polarography in the assay of oxygen diffusing from roots in anaerobic media," *Physiologia Plantarum* 20, 540-553.

_____. (1968). "Oxygen diffusion from the roots of woody species," *Physiologia Plantarum* 21, 539-543.

_____. (1971). "Radial oxygen loss from intact rice roots as affected by distance from the apex, respiration and waterlogging," *Physiologia Plantarum* 25, 192-197.

Armstrong, W., and Boatman, D. J. (1967). "Some field observation relating the growth of bog plants to conditions of soil aeration," *Journal of Ecology* 55, 101-110.

Bacha, R. E., and Hossner, L. R. (1977). "Characteristics of coatings formed on rice roots as affected by iron and manganese additions," *Soil Science Society of America Journal* 41, 931-935.

Bartlett, R. J. (1961). "Iron oxidation proximate to plant roots," *Soil Science* 92, 372-379.

Boone, C. M., Bristow, J. M., and van Loon, G. W. (1983). "The relative efficiency of ionic iron (III) and iron (II) utilization by the rice plant," *Journal of Plant Nutrition* 6(3), 201-218.

Chen, C. C., Dixon, J. B., and Turner, F. T. (1980a). "Iron coatings on rice roots: Morphology and models of development," *Journal of the Soil Science Society of America* 44, 1113-1119.

_____. (1980b). "Iron coatings on rice roots: Mineralogy and quantity influencing factors," *Journal of Soil Science Society of America* 44, 635-639.

Coult, D. A., and Vallance, K. B. (1958). "Observation on the gaseous exchange which takes place between *Menyanthes trifoliata* L. and its environment. Part II," *Journal of Experimental Botany* 9, 390-402.

Crowder, A. A., and Macfie, S. M. (1986). "Seasonal deposition of ferric hydroxide plaque on roots of wetland plants," *Canadian Journal of Botany* 64, 2120-2121.

Gambrell, R. P., and Patrick, W. H., Jr. (1978). "Chemical and microbiological properties of anaerobic soils and sediments." *Plant life in anaerobic environments*. D. D. Hook and R. M. M. Crawford, ed., Ann Arbor Press, Ann Arbor, MI, 119-136.

Ghiorse, W. C. (1984). "Biology of iron- and manganese-depositing bacteria," *Annual Review of Microbiology* 38, 515-550.

Good, B. J., Faulkner, S. P., and Patrick, W. H., Jr. (1986). "Evaluation of green ash root responses as a soil wetness indicator," *Soil Science Society of America Journal* 50, 1570-1575.

Green, M. S., and Etherington, J. R. (1977). "Oxidation of ferrous iron by rice (*Oryza sativa L.*) roots: A Mechanism for waterlogging tolerance," *Journal of Experimental Botany* 28(104), 678-690.

Howeler, R. H. (1973). "Iron-induced organizing disease of rice in relation to physiochemical changes in a flooded oxisol," *Soil Sci. Soc. Amer. Proc.* 37, 898-903.

Johnson-Green, P. C. (1988). "Interactions between the rhizoplans microflora and irone oxide deposition on rice (*Oryza sativa*) roots," M.S. thesis, Queen's University, Kingston, Ontario, Canada.

Joshi, M. M., Ibrahim, I. K. A., Hollis, J. P. (1973). "Oxygen release from rice seedlings," *Physiologia Plantarum* 29, 269-271.

Laan, P., Smolders, A., Blom, C. W. P. M., and Armstrong, W. (1989). "The relative roles of internal aeration, radical oxygen losses, iron exclusion and nutrient balances in flood-tolerance of rumer species," *Acta Bot. Neerl.* 38(2), 131-145.

Mendelssohn, I. A., and Postek, M. T. (1982). "Elemental analysis of deposits on the roots of *Spartina alterniflora* Loisel," *American Journal of Botany* 69(6), 904-912.

Mitsui, S., Kumazawa, K., Yazaki, J., Hirata, H., and Ishizuka, K. (1962). "Dynamic aspects of N, P, K uptake and O_2 secretion in relation to the metabolic pathways within the plant roots," *Soils Science and Plant Nutrition* 8, 25-30.

Okuda, A., and Takahashi, E. (1965). "The role of Silicon." *Mineral nutrition of the rice plant.* The Johns Hopkins Press, Baltimore, MD, 123-146.

Otte, M. L., Rozema, J., Koster, L., Haarsma, M. S., and Broekman, R. A. (1989). "Iron plaque on roots of *Aster tripolium* L.: Interaction with zinc uptake," *New Phytologist* 111, 309-317.

Schwertmann, U., and Taylor, R. M. (1977). "Iron Oxides." *Minerals in soil environments.* J. B. Dixon and S. B. Wead, ed., Soil Science Society of America, Madison, WI, 145-180.

Schwertmann, U., and Thalmann, H. (1976). "The influence of [Fe (II)], [Si], and pH on the formation of lepidocrocite and ferrihydrite during oxidation of aqueous FeCl2 solutions," *Clay Minerals* 11, 189-200.

St-Cyr, L., and Crowder, A. A. (1987). "Relation between Fe, Mn, Cu, Zn, in root plaque and leaves of *Phragmites australis*." *Heavy metals in the environment.* Volume I., S. E. Lindberg and T. C. Hutchinson, ed., 466-468.

_____. (1988). "Iron oxide deposits on the roots of *Phragmites australis* related to the iron bound to carbonates in the soil," *J. of Plant Nutrition* 11(6-11), 1253-1261.

_____. (1989). "Factors affecting iron plaque on the roots of *Phragmites australis* (cav.) Trin ex Steudel," *Plant and Soil* 116, 85-93.

_____. (1990). "Manganese and copper in the root plaque of *Phragmites australis* (Cav.) Trin ex Steudal," *Soil Science* 149(4), 191-198.

Takijima, Y. (1965). "Studies on the mechanism of root damage of rice plants in the peat paddy fields (part 2). Status of roots in the rhyzosphere and occurrence of root damage," *Soil Sci. and Plant Nutrition* 11(5), 20-27.

Tanaka, A., Loe, R., and Navasero, S. A. (1966). "Some mechanism involved in the development of iron toxicity symptoms in the rice plant," *Soil Science and Plant Nutrition* 12(4), 29-33.

Taylor, G. J., and Crowder, A. A. (1983). "Use of the DCB technique for extractions of hydrous iron oxides from roots of wetland plants," *Amer. J. Bot.* 70, 1254-1257.

Taylor, G. J., Crowder, A. A., and Rodden, R. (1984). "Formation and morphology of an iron plaque on the roots of *Typha latifolia* L. Grown in Solution Culture," *American Journal of Botany* 71(5), 666-675.

Trolldenier, G. (1988). "Visualization of oxidizing power of rice roots and of possible participation of bacteria in iron deposition," *Z. Pflanzenernahr. Boden K.* 151, 117-121.

Vale, C., Catarino, F., Cortesao, C., and Cacador, M. I. (1988). "Presence of metal-rich rhizoconcretions on the roots of *Spartina mariuma* from salt marshes Tagus estuary," International Symposium on the Fate and Effects of Toxic Chemicals in large rivers and their estuaries, Quebec, Canada.

van Raalte, M. H. (1944). "On the oxidation of the environment by the roots of rice (*Oryza sativa* L.)," *Hort. Bot. Bogoriensis, Java Syokubutu-Iho* 1, 15-34.

Wallace, A., Shannon, L. M., Lunt, O. R., and Impey, R. L. (1957). "Some aspects of the use of metal chelates as micronutrient fertilizer sources," *Soil Sci.* 84, 27-41.

Wright, R. J., and Hossner, L. R. (1984). "Cultivar differences in iron coatings formed on rice roots," *Cereal Research Communications* 12(3-4), 265-266.

Appendix A
Annotated Bibliography

Armstrong, J., and Armstrong, W. (1988). "*Phragmites australis* - A preliminary study of soil-oxidizing sites and internal gas transport pathways," *New Phytologist* 108, 373-382.

The purpose of this study was to identify plant underground oxidizing sites using a methylene blue dye technique, and to investigate the aeration pathways within the plant by pressurized flow of gases and by anatomical studies. Oxygen release from underground parts was most rapid from young adventitious and secondary roots and particularly basal tufts of fine laterals. Zones of oxidation also occurred around the sprouting tips of horizontal and vertical rhizomes. Dormant tips showed very little oxidizing power, while rhizomes themselves and the older parts of adventitious roots showed none.

Armstrong, W., and Boatman, D. J. (1967). "Some field observations relating the growth of bog plants to conditions of soil aerations," *Journal of Ecology* 55, 101-110.

The objective of this research was to explain differences in the growth of bog plants in the field to soil aeration condition as indicated by soil oxygen diffusion rates, redox potentials, and hydrogen sulfide concentrations. Relative to this review, the authors observed that all species (*Molinia caerulea, Menyanthes, Narthecium, Carex rostrata, Phragmites, Myrica,* and *Potomogeton polygonifolius*) exhibited oxidized iron deposits on their roots. Stagnant soil water conditions were found to reduce plant growth.

Bacha, R. E., and Hossner, L. R. (1977). "Characteristics of coatings formed on rice roots as affected by iron and manganese additions," *Soil Science Society of America Journal* 41(5), 931-935.

The objectives of this study were to (a) determine the relationship between solution iron and manganese and their accumulation on the surface of rice (*Oryza Sativa* L. "Brazos") roots and (b) examine by scanning electron microscopy and x-ray diffraction the morphology and mineralogical composition of the coatings. Rice plants were grown in flooded sand and

subjected to iron (0, 3.3, 16.7, and 33.3 ppm) and manganese (0, 0.67, 3.33, and 6.67 ppm) plus nutrient solution for 30 days. Rice seedlings, in a second experiment, were grown in sand or a Crowley fine sandy loam soil. Root coatings from these plants were removed and used for x-ray diffraction analysis. Root coatings were extracted with citrate-bicarbonate dithionite solution. Growth solution pH ranged from 6 to 7. Scanning electron micrographs showed precipitates on the root surfaces. Analysis of the extracted root coating showed that they consisted primarily of iron; manganese was detected only when solution concentrations were 71.0 ppm. Iron deposition on the root epidermis was 43 times greater than manganese. Iron and manganese coatings were positively correlated with iron and manganese solution concentration ($r^2 = 0.50^{**}$ $r^2 = 0.72^{**}$, respectively). X-ray diffraction analysis of the coatings identified the iron oxide mineral lepidocrocite (gamma - FeOOH) as the only crystalline component of the coatings. The soil experiment produced more lepidocrocite than the sand experiment.

Bartlett, R. J. (1961). "Iron oxidation proximate to plant roots," *Soil Science* 92, 372-379.

The objective of this study was to characterize rhizosphere oxidation of Fe^{2+} in a number of forage crops and natural herbs. Oxidation of iron was demonstrated directly in solution culture, and indirectly in soil by a method involving extraction of ferrous iron. Iron precipitation on plant roots was not measured directly. Reed canary grass, timothy, and trefoil were consistently among the most successful oxidizers, red clover and bromegrass of lesser ability, and alfalfa having the lowest oxidizing ability. In general, poor oxidizers took up the most iron in their tissue. Oxidation was lessened especially in trefoil and alfalfa and to some extent in timothy and canary grass when placed in the dark. Photosynthetic oxygen production may be important in providing aeration in these plants.

Boone, C. M., Bristow, J. M., and van Loon, G. W. (1983). "The relative efficiency of ionic iron (III) and iron (II) utilization by the rice plant," *Journal of Plant Nutrition* 6(3) 201-218.

The paper investigates the counterbalancing effects of iron (Fe^{3+}) reduction with iron (Fe^{2+}) oxidation on iron uptake at the root surface. A series of experiments were conducted to assess iron uptake, reduction, and oxidation. Relative to iron plaque formation, when rice plants were exposed to Fe-EDTA, little iron precipitated on the roots. However, when Fe^{2+} or Fe^{3+} was the iron source, considerable iron plaque formation resulted; as culture solution pH was increased from 3.0 to 5.3, iron plaque concentrations increased, especially when Fe^{2+} was the iron source. These authors suggest that the degree to which the rice rhizosphere contains oxidized iron is dependent on the net effect of the oxidizing power of the rice root and its reducing capacity (from release of root reductants and pH effects).

Chen, C. C., Dixon, J. B., and Turner, F. T. (1980a). "Iron coatings on rice roots: Morphology and models of development," *Journal of the Soil Science Society of America* 44, 1113-1119.

Scanning electron microscopy and X-ray microanalysis were employed to determine microscopic and chemical properties of iron coating on rice (*Oryza sativa* L. "Brazos" cultivar) roots during plant growth and maturity. Root samples were collected from mature field plants growing in (a) a Katy fine sand loam (pH = 6.3) at Katy, TX, and (b) a Beaumont clay (pH = 6.2) at Beaumont, TX, at three different growth stages: 1 week after field flooding, at panicle differentiation, and at heading. Random subsamples of four to six roots were frozen in liquid nitrogen, freeze-dried, and used for scanning electron microscope and energy dispersive x-ray analyses. Rice root coatings were visible about 1 week after flooding as a brownish discoloration that thickens with age of the root. It was hypothesized that these coatings do not interfere with nutrient uptake since no coatings were found on younger parts of major roots near their tips or on young secondary roots, which are critical regions for nutrient uptake. Coating material occurs primarily as fillings (casts) in exposed cavities of the epidermal cells. X-ray microanalysis identified these casts as primarily iron compounds. Two models for cast formation based on whether iron precipitates before or after cell wall decomposition are presented and explain the differences seen in cast morphology, i.e. (a) either hollow interior, smooth surface polyhedral casts or (b) solid interior, rough surface polyhedral casts.

Chen, C. C., Dixon, J. B., and Turner, F. T. (1980b). "Iron coatings on rice roots: Mineralogy and quantity influencing factors," *Journal of Soil Science Society of America* 44, 635-639.

The objective of this study were to (a) determine the effect of rice growth stage, rice cultivar, and soil type of quantities of iron coatings and (b) purify iron compounds from root samples by high gradient magnetic separation for identification by x-ray diffraction analysis. Root samples for iron coating analyses were collected (a) from the rice cultivars "Labelle," "Lebonnet," "Bluebelle," and "Brazos" growing in a Beaumont clay after 1 week of flooding, panicle differentiation, heading, maturity and 4 weeks after harvesting and (b) at maturity from the four cultivars grown at four different locations, with different soils: (a) Lake Charles clay at Bay City, TX, (b) Beaumont clay at Beaumont, (c) Crowley very fine sandy loam at Eagle Lake, MS, and (d) Katy fine sandy loam at Katy. Rice cultivar, growth stage, and soil type were significantly related to the amount of iron oxyhydroxide (FeOOH) on field grown rice roots. Rice cultivar and growth stage significantly interacted to control iron coatings. Accumulation of FeOOH was <2 percent of dry root weight 7 days after flooding of the soil, increased to a maximum of about 10 percent at plant maturity, and decreased slightly thereafter. Soils with a higher clay content, Lake Charles and Beaumont (two vertisols), exhibited less root iron coating than the two soils, Crowley and Katy (alfisols), with lower clay content. High clay content may inhibit iron coating because of (a) binding some iron as

exchangeable cations and (b) providing a more reduced soil environment and thus compensating for the oxidative power of the roots. The "Brazos" cultivar had the largest O_2 release rate from the roots and highest iron coatings on three of the four soils. Both lepidocrocite (gamma-FeOOH) and goethite (alpha-FeOOH) were identified in rice root coatings. This was the first time goethite had been identified on root coatings. Its presence may be due to the following: (a) under rapid oxidation of Fe^{2+} iron, lepidocrocite tends to form, but in time dissolves and the more stable goethite forms, (b) high CO_2 in soil favors goethite over lepidocrocite, and (c) aluminum in solution suppresses the formation of lepidocrocite and goethite tends to form. Oxygen release rates from the roots had a significant effect on the formation of iron coatings, i.e., the greater the release, the greater the amount of FeOOH.

Chino, M., and Baba, A. (1976). "Electron microprobe analysis of zinc and other elements within and around rice root grown in flooded soil," *Soil Science and Plant Nutrition* 22(4), 445-457.

The objective of this study was to identify the distribution of zinc, calcium, sulfur, and phosphorus within and around the rice root. *Oryza sativa* plants were grown in a flooded soil, the soil and roots fixed, and analyzed with an electronprobe x-ray microanalyzer. In the basal region of the root, the elements accumulated in the cells of the epidermis, exodermis, endodermis, and marginal layers of the stele. Zinc and phosphorus appeared to be associated possibly as zinc phosphate. In the apical region, all elements but calcium were highly and evenly distributed in the central part of the root and scarcely found in marginal layers. Calcium was not detected in the apical region. The concentration of an element in the vicinity of the root was found to be approximately equal to that in the other parts of the soil. No characteristic distribution of the elements in the soil-root interfaces was found.

Crowder, A. A., and Macfie, S. M. (1986). "Seasonal deposition of ferric hydroxide plaque on roots of wetland plants," *Canadian Journal of Botany* 64, 2120-2121.

The objective of this study was to document the phenology of plaque formation on the roots of *typha latifolia* in several wetlands and on *Carex rostrata*, *Phragmites australis*, and *T. latifolia* where all three species co-occur. Deposition of ferric hydroxide on *T. latifolia* roots was seasonal in three of the seven marshes sampled, with no seasonal variation in the remaining four marshes. In addition, the four sites showing no seasonal variation in plaque accumulation also exhibited low amounts of plaque in comparison to the other three marshes, which were located adjacent to free-moving water (St-Cyr and Crowder 1989). Plaque formation at these three sites showed rapid deposition in June and July, leveling off in July and August. Site characteristics of pH and Eh were not closely correlated with plaque formation, suggesting that other factors play a more important role.

However, the seasonal peak in plaque accumulation corresponded with the seasonal peak in productivity and aboveground biomass for the three species. The authors suggest that root radial oxygen loss and photosynthetic production of oxygen may be important in determining plaque formation. Although all three plant species accumulated plaque, *Carex* accumulated plaque at a greater rate and to a higher level than did *Typha*. *Phragmites* was intermediate.

Good, B. J., Faulkner, S. P., and Patrick, W. H., Jr. (1986). "Evaluation of green ash root responses as a soil wetness indicator," *Soil Science Society of America Journal* 50, 1570-1575.

The purpose of this study was to determine the effectiveness of root data, including root coatings and root anaerobic respiration, as indicators of waterlogged soil conditions in bottomland hardwood habitats. Green ash (*Fraxinus pennsylvanica* Marsh.) seedlings were transplanted to plots, categorized as "wet" or "mesic" based on soil wetness data, along four bottomland hardwood transects in Louisiana. Root-coating constituents (aluminum, arsenic, calcium, iron, potassium, manganese, nickel, phosphorus, and zinc) and root alcohol dehydrogenase activity, an indicator of the potential for anaerobic metabolism, of the seedlings were measured after 1.5 years. Iron and manganese root coatings were seven and four times greater, respectively, for seedlings growing in wet plots compared with mesic plots. However, a large variance diminished their effectiveness as predictors of waterlogged soils. However, the iron/manganese ratio proved much more suitable and was selected as a predictor variable. The authors concluded that root coatings and, to a lesser extent, anaerobic respiration were different enough between wet and mesic sites to be useful in the development of a model for site wetness classification.

Green, M. S., and Etherington, J. R. (1977). "Oxidation of ferrous iron by rice (*Oryza sativa* L.) roots: A mechanism for waterlogging tolerance," *Journal of Experimental Botany* 28(104), 678-690.

The objective of this study was to characterize iron deposition on and in the roots of rice. Seedlings of rice were exposed to 10, 20, 40, 80, 160, and 320 mg l^{-1} of ferrous iron Fe^{2+} in deoxygenated agar gels containing diluted Hoagland's nutrient solution. Analysis of root deposits were made with light and electron microscopy and electron probe analysis. Iron was deposited both on the surface of and within the root. Iron deposition increased with increasing Fe^{2+} in the agar gel. Iron was found adhering to the root surfaces and to root hairs, and extended to and throughout the outer cortex in cell walls and intercellular spaces. Iron was also found on the tissue diaphragms that traverse the cortex of the root, connecting its outer cortex with the stele. Electron microprobe analysis confirmed that iron was the main constituent of these coatings. Gaseous oxygen diffusing through the cortical air spaces from the aerial part of the plant was suggested as being responsible for the oxidation and precipitation of iron.

Howeler, R. H. (1973). "Iron-induced oranging disease of rice in relation to physio-chemical changes in a flooded oxisol," *Soil Sci. Soc. Amer. Proc.* 37, 898-903.

The objectives of this study were to (a) determine the cause of oranging disease in rice and (b) test cultural practices to alleviate the problem. Seven-day-old rice seedlings were grown in six different soils under different flooding conditions in two experiments. Changes in pH, Eh, and iron and manganese levels in soil solutions after flooding were evaluated and related to the onset of oranging disease. Oranging symptoms were observed to occur as solution iron concentrations increased. From visual observation, coatings on the roots begin as iron concentrations in solution increase. The orange coating of the roots increased in intensity with time until all roots were dark orange to brown and no active white roots remained. The conclusion was made that the oranging disease results from iron-induced nutrient deficiencies. The high iron level in solution inhibits the formation of new absorbing roots, and the root coatings may reduce nutrient absorption capacity.

Laan, P., Smolders, A., Bloom, C. W. P. M., and Armstrong, W. (1989). "The relative roles of internal aeration, radial oxygen losses, iron exclusion and nutrient balances in flood-tolerance of *Rumex* species," *Acta Bot. Neerl.* 38(2), 131-145.

Radial oxygen losses (ROL), determined with cylindrical Pt electrodes and methylene blue assays, from the roots of three *Rumex* species were compared. ROL were higher in the flood tolerant *R. maritimus* and *R. crispus* than in the intolerant *R. thyrsiflorus*. Root iron plaque formation, however, occurred for all three species. In fact, the species with the lowest ROL had the greatest amount of plaque formation (per gram fresh weight of root tissue). Therefore, quantitative differences in root iron plaque formation are not necessarily correlated with ROL or flood tolerance. The more flood-tolerant species had greater root porosity, higher O_2 concentrations at the root apex, greater ROL, and greater root growth than the less flood-tolerant species.

Mendelssohn, I. A., and Postek, M. T. (1982). "Elemental analysis of deposits on the roots of *Spartina alterniflora* Loisel," *American Journal of Botany* 69(6), 904-912.

The objectives of this study were (a) to evaluate the extent to which the rhizosphere of *Spartina alterniflora* is important in precipitating iron and manganese and (b) to determine any difference in the intensity of precipitation as a function of location (streamside versus inland). Root samples were collected in both the streamside and inland zones of a salt marsh in South Louisiana and root coatings observed with light and scanning electron microscopy. The elemental analysis of the root coatings were conducted with x-ray microanalysis and atomic absorption spectrophotometry after citrate-dithionite extraction from the root surfaces. Approximately 50

times more iron was found on streamside roots compared with roots from inland plants. Iron coatings were restricted to the outer cell wall of the epidermis and were composed primarily of iron. Manganese was a minor component of the coatings. The authors proposed that the greater iron precipitation on the streamside roots was primarily due to greater radial oxygen loss from streamside plants, a lower soil oxygen demand in the streamside zone, and somewhat higher iron concentrations in the soil of this zone.

Okuda, A., and Takahashi, E. (1964). "The role of silicon," *The Mineral nutrition of the rice plant.* A. Tanaka et al., ed., The John Hopkins Press, Baltimore, MD 63-73.

The authors found that Fe^{2+} and Mn^{2+} become readily oxidized on the surface of rice roots. Silicon-supplied plants precipitated more iron on their roots than silicon-deficient plants. They proposed that silicon may promote the oxidizing capacity of rice roots. The silicon reduces excessive iron uptake and reduces iron toxicity.

Otte, M. L., Rozema, J., Koster, L., Haarsma, M. S., and Broekman, R. A. (1989). "Iron plaque of roots of *Aster tripolium* L.: Interaction with zinc uptake," *New Phytologist III*, 309-317.

The objective of this study was to determine if root iron plaque formation influences the uptake of copper and zinc in *Aster tripolium*. *Aster tripolium* plants and soil were collected from four salt marshes along the Dutch coast and roots extracted with dithionite-citrate-bicarbonate (DCB) and analyzed for iron, zinc, and copper by atomic absorption spectrophotometry. In addition, the effect of iron plaque formation on zinc uptake was determined in a series of experiments. *Aster tripolium* readily forms iron plaque precipitates on its roots. Both zinc and copper are associated with these root iron plaques. Zinc and copper concentrations of the iron plaque were up to 680 and 2,900 times higher than in the surrounding sediment, respectively. Zinc concentrations in field sampled roots were positively correlated with the amount of zinc on the roots and zinc concentration in the soil, whereas copper concentrations in the roots were only significantly correlated with copper concentrations in the soil. Zinc-uptake experiments demonstrated root surface iron concentrations between 500 and 2,000 nmol iron cm^{-2} enhanced zinc uptake, while higher concentrations reduced uptake. Copper uptake appears not to be affected by plaque formation.

St-Cyr, L., and Crowder, A. A. (1987). "Relation between Fe, Mn, Cu, and Zn in root plaque and leaves of *Phragmites australis*. *Heavy metals in the environment.* Volume I, S. E. Lindberg and T. Hutchinson, ed., 466-468.

This study tested the hypotheses that root "iron plaque" can be a protective mechanism in *Phragmites australis* against the uptake of compounds such as iron, manganese, copper, and zinc. Plant root and leaf samples were collected at five sampling sites ranging from dry land to wetland and

unpolluted to polluted, located in south Ontario and Quebec, Canada, in August 1984. Root plaques were extracted with the cold dithionite-citrate-bicarbonate technique and metals analyzed by atomic absorption spectrophotometry. Leaf samples were pressure digested in nitric acid and hydrogen peroxide and metals analyzed as above. Iron, manganese, copper, and zinc were precipitated on the root surfaces. Positive correlations existed between plaque concentrations of iron, manganese, copper, and root concentration (after plaque metals were removed). Thus, the more of any of these metals precipitated on the root, the more there is taken up by the root. In addition, total metal concentration of iron, manganese, copper, and zinc in the root was positively correlated with the concentration of these metals in the leaf. Therefore, rhizosphere oxidation of these metals does not impede their accumulation in the plant tissue.

St-Cyr, L., and Crowder A. A. (1988). "Iron oxide deposits on the roots of *Phragmites australis* related to the iron bound to carbonates in the soil," *Journal of Plant Nutrition* 2(6-11), 1253-1261.

The purpose of this study was to determine the form of sediment iron responsible for root iron plaque formation. The authors conducted a sequential extraction of iron from wetland soils dividing the total iron into five main fractions: (a) exchangeable iron ($MgCl_2$, pH 7.0), (b) iron bound to carbonates (NaOAC/HOAC, pH 5.0), (C) iron bound (or in) the iron- and manganese-oxides (NH_2OH·HC1 in 28 percent HOAC, pH ~2.0), (d) iron bound to organic matter (H_2O_2/HNO_3, pH~2.0, and NH_4OAC), and (e) residual iron (HF and $HC1O_4$). High correlations occurred between iron plaque accumulation (ppm) and the iron bound to carbonate fraction (0.597, $P < .01$ in June, $n = 23$ and 0.775, $P < .001$ in Sept $n = 22$). This was the only significant correlation identified. Siderite ($FeCO_3$) is thought to be the main iron-carbonate mineral. Siderite is not stable under oxidized conditions and becomes goethite (alpha-FeOOH) readily. Under natural conditions, iron plaque is not significantly correlated with exchangeable iron because this fraction in not directly involved, but Fe^{2+} must be transformed to the carbonate bound form before it can be oxidized.

St-Cyr, L., and Crowder, A. A. (1989). "Factors affecting iron plaque on the roots of *Phragmites australis* (cav.) Trin. ex Steudel," *Plant and Soil* 116, 85-93.

The objective of this study was to determine the effect of soil factors on the amount of iron-bound-to-carbonates in the soil. Samples were collected at six sites ranging from dry land to wetland, polluted to unpolluted. No significant correlations were found between iron plaque concentration and soil factors (pH, percent water, percent organic matter, percent clay, and percent carbonates). However, the amounts of iron-bound-to-carbonates fraction of the soil, responsible for iron plaque accumulation, correlated with percent water, percent organic matter, percent clay, and pH of the substrate. Iron-bound-to-carbonates was negatively correlated with pH (ranges 5.0 to 8.0) and positively correlated with percent water. When

partial correlation coefficients were employed, iron-bound-to-carbonates was positively correlated with percent clay ($r = 0.865$, $P < .10$) when percent organic matter was constant and negatively correlated with percent organic matter ($r = -0.823$, $P < .01$) when percent clay was constant. This indicates a competition for iron between clay and organic matter components of the soil. The authors propose that clay can act as an iron reservoir, but the iron liberated from clay can be absorbed on organic matter before being bound to carbonates in the soil. Thus, iron availability controls plaque formation. Sample sites adjacent to free-flowing water had high iron plaque formation on *Phragmites* roots. The carbonates may be derived from the moving water.

St-Cyr, L., and Crowder, A. A. (1990). "Manganese and copper in the root plaque of *Phragmites australis* (cav.) Trin. ex Steudel," *Soil Science* 149(4), 191-198.

The authors analyzed the iron plaque of *Phragmites australis* roots for manganese and copper to investigate whether heavy metals can be effectively retained by the plaque. *Phragmites australis* was collected at six sampling sites, ranging from dry land to wetland and from polluted to unpolluted, located in Southern Quebec and Ontario, Canada, in mid-June and mid-September 1986. Root coatings were extracted with the cold DCB (dithionite-citrate-bicarbonate) technique and the extractant analyzed for iron, manganese, and copper with atomic absorption spectrophotometry. Soil sediment metals were subdivided into five fractions: (a) exchangeable metals, (b) metals bound to carbonates or specifically absorbed, (c) metals bound to iron-manganese oxides, (d) metals bound to organic matter and sulfides, and (e) residual metals. Iron, manganese, and copper in the soils were determined as above. Manganese concentration in the plaque, like that of iron, was correlated with the manganese-bound-to-carbonates of the substrate. The iron:manganese ratio of the plaque resembles the ratio of iron:manganese-bound-to-carbonates of the substrate. This ratio increases with percentage water and decreases with pH. Plants located near flowing water accumulate more manganese (and iron) in the plaque than plants in other habitats through the summer. Copper in the plaque was positively correlated with pH and with plaque iron and manganese.

Takijima, Y. (1965). "Studies on the mechanism of root damage of rice plants in the peat paddy fields (part 2). Status of roots in the rhizosphere and occurrence of root damage," *Soil Science and Plant Nutrition* 11(5), 20-27.

The major objective of this study was to test the effect of various inhibitory substances on root growth and oxidation in rice. Root-oxidizing power was measured by the oxidation of alpha-naphthyamine. The most physiologically active parts of the root (tips) remained white for a long time, not stained brown with iron. Roots growing in reduced soil formed the oxidative rhizosphere surrounding them. In peaty soils, abundant harmful metabolites may reduce the physiological activity of the root, and the oxidized

rhizosphere and iron banding disappear as a result of the strongly reduced condition of the soil. The author suggests that enzymatic oxidation in the root may also contribute in the formation of the oxidized rhizopshere. The relationship between the reducing power of the soil medium and the oxidizing power of the root seems to decide formation and disappearance of the oxidative rhizosphere, which protects roots from soil toxins.

Tanaka, A., Loe, R., and Navasero, S. A. (1966). "Some mechanisms involved in the development of iron toxicity symptoms in the rice plant," *Soil Science and Plant Nutrition* 12(4), 29-33.

This paper discusses the characteristics of iron toxicity symptoms, critical iron percentage, and the distribution pattern of iron in the plant. Radioautograph of a young root, growing in an ^{59}Fe solution, indicated that a large amount of iron accumulated at the root tip and also that some iron was deposited all over the root. Most of the iron was on the surface of the root with little inside the root, but the accumulation at the tip was inside the root. When iron concentrations are high (7,100 ppm), a large amount was deposited on the root surface.

Taylor, G. J., and Crowder, A. A. (1983). "Use of the DCB technique for extractions of hydrous iron oxides from roots of wetland plants," *American Journal of Botany* 70, 1254-1257.

This study compared the effectiveness of dithionite-citrate-bicarbonate (DCB) technique with synthetic chelates (EDTA and DTPA) for extracting ferric oxyhydroxides from plant roots. *Phragmites communis* collected from the field and with red roots contained iron in these red coatings. DCB extracted more iron than the synthetic chelates.

Taylor, G. J., Crowder, A. A., and Rodden, R. (1984). "Formation and morphology of an iron plaque on the roots of *Typha latifolia* L. grown in solution culture," *American Journal of Botany* 71(5), 666-675.

This paper investigates some of the chemical parameters affecting plaque formation and describes the morphology of the resulting iron plaques. *Typha latifolia* plants were grown hydroponically in full strength Hoagland's nutrient solution (pH 5.5) with 5 ppm Fe-EDTA and then subjected to experimental conditions to test the effects of (a) iron source (Fe^{2+} as $FeSO_4$, Fe-$(BPDS)_3$ (ferrous-4, 7-di (4-phenylsulfonate 1. 10-phenanthroline, Fe^{3+} as $FeCl_3$, Fe-EDTA, Fe-EDDHA (ferric ethylenediamine-di(0-hydroxphenylacetic acid), (b) Fe^{2+} concentration (5, 10, 20, 50, 75, or 100 ppm as $FeSO_4$), and (c) pH from 3.0 to 5.0. Solutions were maintained hypoxic with N_2 gas. Greatest plaque formation occurred when Fe^{2+} was the iron source indicating that plaque formation is dependent on the oxidation of Fe^{2+} to Fe^{3+}. Little plaque formed on *Typha* roots when Fe^{3+} or chelated iron was used as the iron source. The extent of plaque formation increased with the concentration of Fe^{2+} in solution and with pH in the range of 3.0 to 4.6. Above pH 4.6, oxidation of iron may

have reduced precipitation on the root surface. Plant development was most extensive approximately 1 cm from the root tip, but all root surfaces showed some iron staining.

Trolldenier, G. (1988). "Visualization of oxidizing power of rice roots and of possible participation of bacteria in iron deposition," *Z. Pfanzenernähr Bodenk* 151, 117-121.

This study investigated the oxidizing power of rice roots in different media. Plants preadapted in nutrient solution were embedded in semisolid agar medium to observe oxidation of ferrous iron cations and leuco methylene blue as well as solubilization of ferrous sulfide. All experiments demonstrated root-oxidizing power. Iron was deposited on and around the root. Bacterial colonies could be identified in the rhizosphere and on the root surfaces. The results suggest participation of bacteria in ferric iron deposition rhizosphere of rice.

Wallace, A., Shannon, L. M., Lunt, O. R., and Impey, R. L. (1957). "Some aspects of the use of metal chelates as micronutrient fertilizer sources," *Soil Science* 84, 27-41.

This paper summarizes research on reactions of chelates in soils and plants and on methods of application. When soybeans were grown in sand culture with nutrient solution containing different levels of iron as sulfate and EDDHA, iron chelate of EDDHA (ethylenediamine di(0-hydroxphenylacetic acid)) resulted in less fixation of iron on roots than did $FeSO_4$.

Wright, R. J., and Hossner, L. R. (1984). "Cultivar differences in iron coatings formed on rice roots," *Cereal Research Communications* 12(3-4), 265-266.

The objective of this study was to determine the relationship between O_2 release rates and formation of iron coatings in rice cultivars with different O_2 release rates. Flooding caused the soil Eh values to rapidly decrease to −160 mV. Although the cultivar with the highest O_2 release rate had the highest concentration of iron precipitated on its roots, when all cultivars were considered, O_2 release rate was not significantly correlated with root coatings. Therefore, conclusive evidence identifying the importance of root oxygen release and iron plaque formation was not generated by this study. However, the relatively short time of the experiment (32 days) and the low iron concentrations in solution may have contributed to this finding.

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

Reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503.

1. AGENCY USE ONLY *(Leave blank)*

2. REPORT DATE
August 1993

3. REPORT TYPE AND DATES COVERED
Final report

4. TITLE AND SUBTITLE
Factors Controlling the Formation of Oxidized Root Channels: A Review and Annotated Bibliography

5. FUNDING NUMBERS

6. AUTHOR(S)
Irving A. Mendelssohn

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
Wetland Biogeochemistry Institute
Center for Coastal, Energy and Environmental Resources
Louisiana State University, Baton Rouge, LA 70803

8. PERFORMING ORGANIZATION REPORT NUMBER
Technical Report WRP-DE-5

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
U.S. Army Corps of Engineers, Washington, DC 20314-1000
U.S. Army Engineer Waterways Experiment Station, Environmental Laboratory, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES
Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161.

12a. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution is unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT *(Maximum 200 words)*

Although root plaques and associated oxidized root channels are used for wetland identification as field indicators of wetland hydrology, little information is available concerning their reliability and the environmental and biotic factors controlling their formation. Therefore, the objectives of this study were to (a) provide an annotated bibliography of literature concerning root iron plaques, (b) describe and evaluate the current state of knowledge of the factors controlling the formation of iron plaques, and (c) recommend research to address information gaps.

Both abiotic and biotic factors control the presence and degree of iron plaque formation. The most important abiotic factor is the availability of soil iron. However, the effect of site-variation in soil physico-chemical characteristics, e.g., texture, organic matter, pH, Eh, and soil fertility, on iron availability and the formation and persistence of root plaque and oxidized root channels have not been adequately investigated. Although the oxidizing capacity of the plant root is the most important biotic factor controlling plaque formation, only a limited number of wetland species have been evaluated for this ability; therefore, species-specific differences are generally unknown.

Unlike some of the other hydrologic indicators used in wetland delineation (e.g., water marks on trees or sediment deposits), root plaques and oxidized root channels indicate soil saturation for a sufficient period to produce anaerobic soil conditions.

(Continued)

14. SUBJECT TERMS

Iron plaque	Root oxygen loss	Wetland hydrologic indicators
Root concretions	Water logging	
Root deposits	Wetland delineation	

15. NUMBER OF PAGES
36

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
UNCLASSIFIED	UNCLASSIFIED		

13. (Concluded).

Additionally, when found in conjunction with a living root, oxidized root channels indicate that the anaerobic conditions occurred within the life span of the plant root. Therefore, the presence of oxidized root channels and iron plaque surrounding living roots is a relatively good indicator of wetland hydrologic conditions. However, until more is known about the relative abilities of different plant species to produce oxidized root channels, the temporal persistence of the root iron plaque, and the role soil chemistry plays in controlling plaque formation, the absence of oxidized root channels, in itself, should not be used to indicate the absence of a wetland.